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Review

In search of Paleolithic dogs: a quest with mixed results

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ABSTRACT

Archaeological evidence has long placed the origins of the domestic dog (*Canis lupus familiaris*) just prior to the beginning of the Holocene Epoch, some 12,000–15,000 years ago. Some studies of genetic profiles of modern canids have, however, suggested a much earlier origin, dating to Paleolithic times and perhaps exceeding 100,000 years. With such studies as a backdrop, cases have been made recently on archaeological grounds for Paleolithic dogs that in certain cases exceed 30,000 years old. When examined systematically, however, some such studies exhibit conceptual and methodological flaws, calling into serious question the accuracy of the cases advanced. At least one recent study highlights that difficulty. When a series of cases for putative Paleolithic dogs is assessed, convincing cases for such dogs are confined to about the past 15,000 years, or latest Paleolithic times. Further developments on certain specific fronts may change that, but for the time being the longstanding archaeological understanding of the dog domestication time frame continues to be reasonably accurate. Recent molecular genetic studies are converging on that temporal framework as well. Archaeologists need not be automatically swayed by ongoing changes in molecular genetic profiles.

1. Introduction

The origin of the domestic dog (*Canis lupus familiaris*) has usually been placed just before the beginning of the Holocene Epoch, some 12–15,000 years ago. That inference has been based especially on skeletal remains at archaeological sites that show modest but appreciable size reduction and morphological divergence compared to wild wolves (*C. lupus*), the ancestral species, after that time frame. Recent years, however, have brought some studies that make a case for much older skeletal remains of dogs, in some cases exceeding 30,000 years old (e.g., Germonpré et al., 2009, 2012; Ovodov et al., 2011). Some of these studies, including follow-up commentary exchanges, have appeared in the pages of this journal. Likely one impetus for developing these cases has been evaluation of the molecular genetic profiles of modern canids that have been used to make a case for even more ancient dog origins, perhaps 100,000 or more years ago as originally formulated (Vilà et al., 1997). Though recent genetic assessments of both modern and ancient canids cast serious doubt on these results (e.g., Thalmann et al., 2013; Freedman et al., 2014), some archaeological evaluations have been influenced by the earlier studies. As such, the cases advanced entail substantial implications for our understanding of dog origins, and also for accurately modeling the course of events in the larger sweep of human prehistory.

Perhaps a blunt observation is in order at the outset. Put simply, making a case for the oldest dogs is guaranteed to be headline news. This factor stems from the close relationship between people and dogs, such that many people are inherently quite interested in the origins of the dog–human association. If it began well before the time frame of the longstanding model, that knowledge qualifies as a prominent finding, of interest to many people beyond the halls of academe.

Significantly, in the pages of this journal Boudadi-Maligne and Escarguel (2014) have recently critiqued some of the cases for earliest dogs, finding them problematical. Boudadi-Maligne and Escarguel's (2014) presentation was restricted to canids from Goyet Cave, Belgium (Germonpré et al., 2009), and Razboinichya Cave Siberia (Ovodov et al., 2011), both exceeding 30,000 years old, along with specimens from Předmostí, the Czech Republic (Germonpré et al., 2012), dating to 26,000–27,000 years BP. Accordingly, there would be little point in dwelling on these cases, though they do merit some observations. While Boudadi-Maligne and Escarguel (2014) have performed a valuable service, their work excluded several other cases made for later Paleolithic dogs, as well as leaving ambiguous the issue of just when canid domestication took place. The current presentation thus seeks to build on Boudadi-Maligne and Escarguel's (2014) effort, by expanding it to include other cases, as well as taking up the issue of canid

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Table 1
Characteristics of reference samples used in Discriminant Function Analysis (DFA) for the taxonomic assessment of several canid specimens, including the partial mandible from Bonn-Oberkassel, Germany (data from Benecke, 1987).

Group	Source/characteristics	Maximum number[a]
Late Paleolithic Wolves	Eurasia	47
Mesolithic Dogs	Europe	15
Recent Wolves	Greenland	12
Recent Wolves	Europe	6
Zoo Wolves	Mus. Natural History, Berlin	6
Dingoes	Mus. Natural History, Berlin	10
Total		96

[a] Because Benecke's DFA incorporated several steps, involving the assessment of several archaeological specimens, reference sample sizes fluctuated according to the objectives, and/or the characteristics of the particular specimen in question.

domestication timing. Moreover, a case emerges that in their zeal to document Paleolithic dogs, some archaeologists have been led to overlook their own field's traditional strengths, and venture into unproductive directions. Perhaps the best way to begin developing that point is to consider a historically convincing case for a Paleolithic dog.

2. Paleolithic dogs? a longstanding convincing case

This section outlines the case of remains from Bonn–Oberkassel in Germany, widely held for years as perhaps the most ancient known evidence of dog, at about 14,000 years old. Accordingly, it is quite late Upper Paleolithic in age. Though originally discovered in the early 1900s, re-evaluation of a partial mandible led Nobis (1979, 1986, 1996) to conclude that domestic dog was represented. His assessment was based especially on the size and proportions of the teeth. Benecke (1987) provided a more definitive re-evaluation as part of a broader assessment of early dog remains from northern Europe. Because he made a convincing case that the Bonn–Oberkassel partial jaw represents a dog, it is worth specifying the terms in which he did that.

Benecke dealt with several linear measurements on the Bonn–Oberkassel jaw and assessed its taxonomic status with the aid of multivariate discriminant function analysis, or DFA. DFA calls for corresponding measurements from individuals of several reference groups, each group potentially representing the case being evaluated, the "unknown." Key to the success of this procedure is that one has in principle appropriate reference groups. Appropriate in this case includes the proviso that membership in those reference groups entails independent justification on theoretical grounds. Table 1 summarizes the composition of Benecke's reference groups. In general, this was a valid series, consisting of different wolves, both modern and Paleolithic, a series of European Mesolithic Period dogs, and even some dingoes. Benecke employed several steps, and DFA classified the Bonn–Oberkassel jaw with the Mesolithic dog group when entered into an analysis as an "unknown." Thus Benecke's work provided a convincing demonstration that the Bonn–Oberkassel specimen almost certainly represents a dog.[1]

Context is relevant too, and it is significant that the Bonn–Oberkassel dog originally accompanied a human double burial (Benecke, 1987; Street, 2002). The fact that it is a burial speaks to the nature of the domestic relationship (Morey, 2006), but it should be borne in mind that morphological criteria were the essential basis for determining it to be, taxonomically speaking, a dog. Moreover, more recently obtained direct dates on bones from this burial confirm that ca. 14,000 cal BP is a reasonable approximation of its antiquity (Hedges et al., 1998: 230; Street, 2002: 270, Table 1; Baales, 2006: 423, Table 2).

3. Paleolithic dogs? Some problematical cases

3.1. The Goyet Cave Canid, Belgium

Boudadi-Maligne and Escarguel (2014) showed that this ca. 36,000 year old canid is almost certainly not a dog, but it is worth noting some key problematical aspects of the original study (Germonpré et al., 2009) that contributed to an erroneous conclusion. First, from the information presented (Germonpré et al., 2009: 474) the skull from Goyet is not even securely linked to the deposits that reflect human activity there. Beyond that consideration, Table 2 provides the composition of DFA reference groups used by Germonpré et al. (2009). In contrast to Benecke's (1987) study, the reference sample of archaeological dogs consists of only five specimens, and two should probably be regarded as tentative identifications. Specifically, reservations about two relatively large late Paleolithic specimens from Eliseevichi I on the Russian Plain (Sablin and Khlopachev, 2002) have been expressed by others (e.g., Miklósi, 2007: 103; Wang and Tedford, 2008: 157; Napierala and Uerpmann, 2012: 132). The other three were smaller in size, still relatively early though postdating the Bonn–Oberkassel dog, and were apparently taxonomically secure.

All other dogs in Germonpré et al.'s (2009) reference series are recent. There were fifty-two in all, divided into two basic groups, as summarized on Table 2. The smaller of those groups (18), called Recent Archaic Dogs, consisted of two breeds, Chow Chows and Siberian Huskies, taken to have ancient origins. The second group, Recent Other Dogs (34), they further subdivided into three smaller subgroups, indicated on Table 2. They then treated those three subgroups as separate groups for their multivariate analyses.

Beyond problematical reference series, Germonpré et al.'s (2009: 476) own words identify an analytical issue: "To reduce the effect of size between the different large canid groups the following indices were used: … ". They then conducted their DFA using indexed data, expressing each dimension as a proportion of

Table 2
Characteristics of reference samples used in Discriminant Function Analysis (DFA) for the taxonomic assessment of Paleolithic canid skulls, including one from Goyet Cave, Belgium (data from Germonpré et al., 2009).

Group	Source/characteristics	Number[a]
Recent Wolves	Belgium, Russia, Caucasus, Jamal, Yakutia, Kamchatka, the Far East	46
Prehistoric Dogs	See text	5
Recent Archaic Dogs	Chow Chows (3) Siberian Huskies (15)	18
Recent Other Dogs		34
A) With Slender Snout	Irish Wolfhounds, Doberman Pinschers	A) 6
B) With Short Tooth Row	Mastiffs, Tibetan Mastiff, Rottweilers, Great Danes	B) 11
C) With Wolf-like Snout	German Shepherd, Malinois	C) 17
Total		103

[a] Numbers indicated here do not always precisely match those given by Germonpré et al. (2009: 475: Table 1). That is because not absolutely all cases listed in their tabular summary were actually used in computing discriminant functions, and excluded specimens are indicated in their text.

[1] A few more bones than just the partial jaw have survived into modern times. Norbert Benecke made this clear in identifying the work of Martin Street (2002) in a personal communication in 2004, but I lost track of that, and in my own work (e.g., Morey, 2010) continued to suggest that only the partial jaw still survives. I regret that error.

Table 3
Sample characteristics for groups of canids yielding cranial measurements plotted in Figs. 1 and 2.

Group	Source/characteristics	Number
Wolves (*Canis lupus*)		
1) *Canis lycaon*[a]	Minnesota, Michigan, Ontario (recent)	57
2) *C. l. baileyi*	Arizona, New Mexico, northern Mexico (recent)	43
3) *C. l. lupus*	Denmark (Holocene)	10
Subtotal		110
Dogs (*C. l. familiaris*)		
1) United States	Eastern/Midwestern U. S., burials, <10,000 years old	47
2) Europe	Denmark, and one from Germany, <10,000 years old	18
Subtotal		65
Total		175

[a] As noted in the text, this canid was previously recognized as a subspecies of *Canis lupus*, *C. l. lycaon*, and as a source of metric data was recognized as such in this author's previous works (e.g., Morey, 1992, 2010).

one other. Using such proportions can be useful for certain purposes, but it is problematical here, beyond established challenges in legitimately using ratios in statistical manipulations (see Baur and Leuenberger, 2011). The reason is that Germonpré et al. (2009) treated morphological features of the skulls as though they vary independently from overall size at a population scale. But they do not because long established principles of allometry mitigate against such (Gould, 1966; see also Morey, 1992), and treating size as independent of morphological characteristics contributed to Germonpré et al.'s (2009) mistaken identification.

Beyond these considerations, a recent assessment of mtDNA from the Goyet canid, in comparison to comparable samples from a substantial series of modern dogs and wolves, resulted in a telling conclusion: "its mtDNA relation to other canids places it as an ancient sister-group to all modern dogs and wolves rather than a direct ancestor of dogs" (Thalmann et al., 2013: 872). Certainly the value of integrating archaeology and genetics, as called for by Larson et al. (2012), is on display there.

3.2. Canid skulls from Předmostí, the Czech Republic

Předmostí is an open air Gravettian site in the Czech Republic that was occupied at different times during the period between about 26,000 and 27,000 BP. As described by Germonpré et al. (2012), the original excavations date back to the 1880s, and this site included a human burial area, along with some portable art objects. There were also numerous mammal remains, dominated by mammoth, followed by large canids. Among those canid remains were seven complete skulls, and Germonpré et al. (2012) assessed three of them as being Paleolithic dogs. Boudadi-Maligne and Escarguel (2014) included this series in their evaluation, finding them to be doubtful, so they need not occupy much attention here. It is worth noting, however, Germonpré et al.'s (2012) analytical methodology.

Like the Germonpré et al. (2009) study, this 2012 study also incorporated multivariate Discriminant Function Analysis (DFA) on cranial measurements. Here, Germonpré et al. (2012) worked with two reference groups of animals designated as archaeological dogs. One group consisted of only three specimens, the three smaller ones from their reference sample of five in the earlier study (Germonpré et al., 2009). These they designated as the "Prehistoric Small Dog" group (Germonpré et al., 2012: 186). In addition, they used a second reference group of five specimens, designated as the "Paleolithic Dog" group (Germonpré et al., 2012: 186). Two of these were the same problematical Eliseevichi I specimens used in the 2009 study. In that study Germonpré et al. (2009) concluded that the Goyet Cave canid, along with two problematical ones, one each from Mezin and Mezhirich on the Russian Plain (see Section 3.5), were Paleolithic dogs. Accordingly, they used all three as established dogs in this new reference group. Thus, the Předmostí crania were determined to be dogs based on affinity to a reference group composed of specimens whose membership lacked convincing justification. Boudadi-Maligne and Escarguel (2014) found it quite doubtful that any Předmostí crania represent dogs.

3.3. Canid skull from Razboinichya Cave, Siberia

This is the final setting formally considered by Boudadi-Maligne and Escarguel (2014), and found by them to be doubtful. In particular, Ovodov et al. (2011) reported on a canid skull and mandibles from Razboinichya Cave in the Altai Mountains of southern Siberia, dating to over 30,000 years ago. They characterized this as an incipient dog, reflecting a domestication process subsequently truncated by Late Glacial Maximum conditions. Problematically, while there are a variety of bones of different species in the deposits, there are no artifacts or other direct evidence of human occupation. The authors note, however, that occasional small charcoal pieces and burnt bones imply that people probably visited the cave, at least occasionally. In terms of size and proportions, Ovodov et al. (2011) found the skull to be extremely similar to relatively large Thule period dogs (ca. 1000 BP and later) from Greenland. At the same time, though, its upper carnassial tooth length is within the size range of modern wolves, and there is no tooth crowding, generally expected in early dogs. Recently, an assessment of genetic affinities through analysis of mtDNA samples from a tooth and bone of this canid (Druzhkova et al., 2013) contributed to the complexity. Finding it removed from sampled wolves, including ancient local ones, the investigators found that "The haplotype derived from the Altai [Razboinichya] specimen clusters among sequences obtained from pre-Columbian dogs and other Late Pleistocene wolf-like canids" (Druzhkova et al., 2013: 4). Their preliminary interpretation was that this specimen is "likely an ancient dog with a shallow divergence from ancient wolves" (Druzhkova et al., 2013: 5). They also found that its haplotype is unique, a circumstance that inevitably complicates such an appraisal. In the same year, however, Thalmann et al. (2013: 872) assessed the mitochondrial genome of this canid, and found that it did "not support recent common ancestry of the Altai specimen lineage with the great majority of modern dogs."

Morphologically, Ovodov et al. (2011) had felt that the evidence pointed to incipient domestic status, rather than simply an aberrant wolf. But given that it's a single individual with ambiguous genetic affinities and several traits consistent with those of a wild canid, and has no clear association with people, this inference is problematical. Another reason for misgivings about the Razboinichya canid, is that prior to the Druzhkova et al. (2013) study, Crockford and Kuzmin, both coauthors of the Ovodov et al. (2011) piece, expressed ongoing reservations about that specimen (Crockford and Kuzmin, 2012: 2800). Significantly, based on their morphological evaluation, (Boudadi-Maligne and Escarguel 2014) also found this specimen doubtful.

3.4. Canid skulls from Eliseevichi 1, the Russian Plain

This site dates to 13,905 BP or ca. 17,000 cal BP (Germonpré et al., 2009: 475). Two isolated skulls from this site were identified by Sablin and Khlopachev (2002) as dogs and, as noted, were part of the reference series used by Germonpré et al. (2009) in their study featuring the Goyet Cave canid. As noted in that summary, these skulls are the subject of significant taxonomic reservations by others (e.g., Miklósi, 2007: 103; Wang and Tedford, 2008: 157;

Napierala and Uerpmann, 2012: 132). For example, Wang and Tedford (2008: 157) found that the ratio of the third premolar crown length to that of the fourth premolar on the one skull where that could be assessed, is consistent with that of a Gray Wolf, not a dog. The skulls were found many years ago in a site area with a variety of artistically rendered objects. Both are adults, and one had a hole in the side of the skull, presumably for extraction of the brain. The skulls may have been curated for symbolic reasons, and while the case for them being dogs is intriguing, the evaluation below (Section 4), renders their status as dogs doubtful.

3.5. Canid skulls from Mezin and Mezhirich, the Russian Plain

In Germonpré et al.'s (2009) study, two skulls beyond the one from Goyet Cave, Belgium, one from Mezin and one from Mezhirich, on the Russian Plain, were also designated as dogs. These were not evaluated by Boudadi-Maligne and Escarguel (2014). Conceptually both are less provocative than the Goyet canid because they are both much younger, some 20,000 years younger (Epigravettian), and unlike the Goyet case, there is no reason to question the association of the skulls with these established human settlements, In addition, the Mezin skull has been singled out previously. As Germonpré et al. (2008: 489, 2009: 481) have noted, one investigator (Pidoplichko, 1998) suggested that it was a dog. Benecke (1987) analyzed that skull (Mezin 5490) with DFA and found it most similar to zoo wolves, the latter showing certain morphological characteristics similar to some domestication changes. Accordingly, he felt that it and a second Mezin skull may represent "an initial stage in the domestication of the wolf" (Benecke, 1987: 47), though not true dogs. Meanwhile, Germonpré et al. (2009) considered two other skulls from Mezin, and assessed them as wolves. But the Mezin and Mezhirich skulls were evaluated directly alongside the Goyet skull, according to identical criteria.

Because of that circumstance, their taxonomic status remains ambiguous, and at most the Mezin and Mezhirich skulls inferred to be dogs might be regarded as possibly transitional between wolf and dog. Benecke's (1987) study did not include anything from Mezhirich, so no comparison is possible there. But the overall ambiguity of the resulting situation has been pointedly noted with reference to the problematical Goyet case: "The proposed earliest evidence of a dog from Goyet (Germonpré et al., 2009) must therefore be evaluated in comparison to non-ambiguous wolves and dogs and not in comparison to other questionable specimens like those of Eliseevichi I, Mezin and Mezhirich" (Napierala and Uerpmann, 2012: 132).

4. Paleolithic dogs? Assessing individual specimens

4.1. Comparative series

Beyond different conceptual issues, it seems worthwhile to evaluate these specimens in replicable terms, for example by comparing them with established series of wolves and dogs (see Table 3). Morey (2010: Appendix A) provides an extensive compilation of metric data on skulls of modern wolves and established archaeological dogs. This presentation draws from that compilation here, but one complication concerns the wolves. In the first place, all from that compilation are North American, not ideal given the Eurasian ancestry of dogs. In addition, they are relatively modest-sized varieties, from temperate and desert southwestern settings. As originally assembled years ago, two subspecies are represented, *Canis lupus lycaon* (temperate, $n = 57$) and *C. l. baileyi* (southwestern, $n = 43$). Moreover, *C. l. lycaon* has been in a state of taxonomic flux, being regarded now by many authorities not as a gray wolf (*C. lupus*), but as a separate species, *Canis lycaon* (see Wilson et al., 2003; Wang and Tedford, 2008: 65). That new standard is replicated here.

As noted, *C. lycaon* is one of the more modest-sized North American wolves, but at least two factors mitigate that complication appreciably. One is that all specimens in the series used here come from the upper Midwest of the United States (Minnesota, Michigan), or from Canada (Ontario). As such, they come from populations of individuals that tend to be somewhat larger than more southerly distributed forms. Related to that factor is that *C. lycaon* in these areas is known to hybridize periodically with individuals of *C. lupus* that inhabit the same area (Chambers et al., 2012). Accordingly, while not optimal samples for the specified reasons, the *C. lycaon* series used here retains greater utility than might be indicated on first glance.

Both *C. lycaon* and *C. l. baileyi* serve a useful purpose here, but since they are not optimal, some data from some European wolves, also collected years ago, appear alongside them. The European wolves consist of a small series of ten Holocene age specimens from Denmark. They are from the collections of the Zoological Museum at the University of Copenhagen, in Denmark. Table 4 presents the raw data on this series. While not every specimen has been reliably dated beyond a general Holocene affiliation, those that have been span almost 8000 years from roughly 10,250–2550 years ago, following the framework of Aaris-Sørensen (1998).

The dogs are all well established archaeological cases dating within the last 10,000 years. There are 65 total, 47 from North America, and 18 from Europe, all but one of those from Denmark. All of the North American dogs were recovered as burials, and the same is true for at least some of the European cases. For both North American wolves and all dogs, raw data are in Morey (2010, Appendix A).

4.2. Comparisons

Fig. 1 shows a bivariate plot of greatest palatal breadth (GPB) by condylobasal length (CL) for several groups of canids, as described above, with the corresponding values for individual archaeological canids under consideration plotted as well (see Table 5). Boudadi-Maligne and Escarguel (2014: 86) have presented a similar plot, using the same variables, incorporating a large series of recent Eurasian wolves. Several findings from these plots warrant recognition. For one thing, using CL, an overall skull length dimension, as

Table 4
Measurements (mm.) on several Holocene *C. lupus* crania from Denmark in the collections of the Zoological Museum, University of Copenhagen, Denmark.

Key[a]	Location	Measurement[b]		
		CL	GPB	LC
5	Ramløse, Frederiksborg Amt.[c]	229	76	25.9
15	Knabstrup, Holbaek Amt.	224	75	27.3
29	Skanderborg, Skanderborg Amt.	244	81	26.7
31	Halleby Aa, Tømmerup Mose, Holbaek Amt.	225	72	25.2
38	Arreskov Sø, Svendborg Amt.	224	79	26.5
39	Barkaer, Randers Amt.	257	86	27.0
45	Hørmested, Hjørring Amt.	240	84	24.6
56	Søderup, Københavns Amt.	220	73	26.0
58	Stenstrup Mose, Praestø Amt.	221	73	25.2
62	Tovbro, Rubjerg, Hjørring Amt.	220	79	24.3
Mean		230.4	77.8	25.87

[a] Numerical key to geographic location and age from Aaris-Sørensen (1977: 130–132).
[b] Measurements in von den Driesch (1976: 42–45): CL = condylobasal length, meas. no. 2; GBP = greatest palatal breath, meas. no. 34; LC = length of the carnassial tooth, P4, meas. no. 18.
[c] Amt., Danish term, corresponds approximately to county in English.

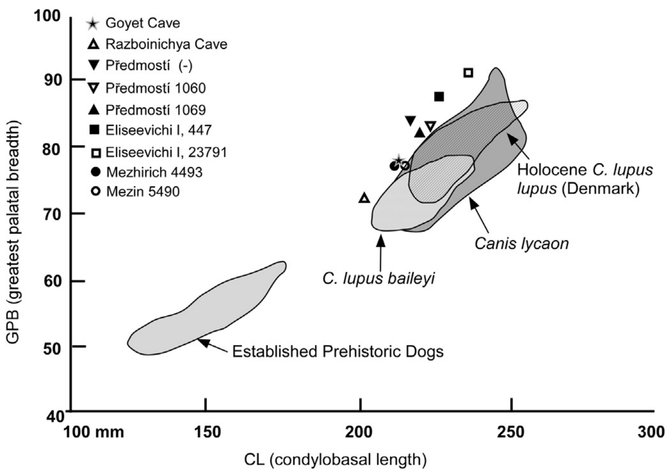

Fig. 1. Bivariate plot of GPB (Greatest Palatal Breadth) by CL (Condylobasal Length) for three groups of modern or Holocene wolves, and one series of established prehistoric dogs, post-dating 10,000 BP, from North America and Europe (measurements defined by von den Driesch, 1976). The contours indicate the range of plotted scores for each group. Superimposed on this plot are the corresponding values for several putative Paleolithic dogs. Using CL as a guide, one can see that the putative Paleolithic dogs are wolf-sized, but have unusually broad palatal dimensions. A comparable plot is provided by Boudadi-Maligne and Escarguel (2014: 86, Fig. 5), based on the same variables and using a larger series of wolves. That plot includes the earliest of the putative Paleolithic dogs considered here (Goyet Cave, Razboinichya Cave, Předmostí), and shows the same basic result.

a basic size guide, all of the putative Paleolithic dogs fall well above the range of established prehistoric dogs. At the same time, however, they fall within the range of recent wolves. Given that, it is also noteworthy that the proportional relationship between the two dimensions for the Paleolithic canids being evaluated is more like established dogs than it is to wolves. Compared to most wolves, dogs do tend to have proportionally wider cranial dimensions (Morey, 1992). Thus, considering the Goyet canid (Germonpré et al., 2009), given modest wolf size, it can be readily appreciated how the relationship between a cranial length and breadth measure was taken to suggest the possibility of a dog. But therein lies the fallacy of treating overall size as though it is independent of morphological characteristics. It is worth emphasizing that while as a group, the putative Paleolithic dogs on Fig. 1 do have unusually wide palatal dimensions, beyond that single morphological trait they are not a meaningful group. Rather, they are a handful of wolf-sized individual specimens from scattered locations, collectively spanning some 20,000 years. Moreover, one of the points stressed by Boudadi-Maligne and Escarguel (2014) in their timely evaluation is the wider range of morphological variation in wolf populations than is generally incorporated.

With that Goyet specimen in particular, its identification as a dog ancestral to recent dogs is not supported, leading to the suggestion that it reflects a domestication episode that was not sustained (Larson et al., 2012: 8878; Thalmann et al., 2013: 872). Perhaps, but the standard principle known as Occam's Razor suggests that a considerably simpler explanation, that the Goyet canid was not a dog, is more likely the case. Accordingly, the suggestion that it represents a not previously recognized form of Pleistocene wolf has also been made (Thalmann et al., 2013: 872), and is far simpler than the idea of an aborted domestication episode.

Either way, though, that the Goyet canid had nothing to do with later dogs, even the questionable ones, is strongly suggested by its relatively small size. Using CL as a guide (see Table 5), it is smaller than the three putative dogs from Předmostí (Germonpré et al., 2012) in the Czech Republic and the two from Eliseevichi 1 in Russia (Sablin and Khlopachev, 2002), all of which date substantially later. It is approximately the same size as those from Mezin and Mezhirich in the Ukraine (Germonpré et al., 2009), even later still (see Table 5). Only the ca. 33,000 year old specimen from Razboinichya Cave in Siberia is slightly smaller, but that specimen's questionable characteristics were noted above, and even it is larger than any established prehistoric dog, and falls within the size range of one known European wolf population (Boudadi-Maligne and Escarguel, 2014: 86, Fig. 5).

Fig. 2 presents another bivariate plot involving the same specimens, but instead of GPB, the dimension plotted against CL is the length of the carnassial tooth (LC), the upper fourth premolar (see Table 5). The relevance of a tooth dimension lies in the longstanding recognition that evolutionary tooth size reduction seems to be delayed relative to other skeletal changes, such that early dogs can be expected to have unusually large teeth, sometimes crowded in the tooth row (e.g., Clutton-Brock, 1995: 16). What this plot shows, however, is that with two exceptions, the putative Paleolithic dogs fall within the range of established wolves. Of the two exceptions, one is Mezhirich 4493, already suggested here as perhaps transitional between wolf and dog. The other is the Razboinichya canid, with a shorter CL than sampled wolves. For present purposes, it is well worth highlighting the placement of the Goyet Cave canid. Germonpré et al. (2009: 488) showed a photograph of the skull in palatal view, drawing direct attention to the “large carnassial of the Goyet dog.” But as Fig. 2 shows, the Goyet Cave canid's carnassial tooth is not particularly large. In short, on morphometric grounds, available data do not support the assessment of these canids as dogs.

5. Paleolithic dogs? Some credible cases

5.1. Pont d'Ambon, Montespan, Le Closeau, Le Morin, France

Pionnier-Capitan et al. (2011) have reported on canid remains from three Late Paleolithic sites in France, Pont d'Ambon, Montespan, and Le Closeau. Forty-nine specimens were identified as dogs, characterized as Late Glacial small dogs. From the associated dated time ranges, certain specimens conceivably approach 15,000 years old, though they may be somewhat younger. In making their identifications, the authors were especially careful to guard against confusing dogs with dholes (*Cuon alpinus*), “a middle-sized Canidae shorter yet sturdier than a wolf the size of which can be similar to early small dogs” (Pionnier-Capitan et al., 2011: 2124). All told, given their small size and documented morphological characteristics, there is little reason to question that these authors have arrived at valid identifications of dogs. Given that, it is also relevant to note that some identified dog bones bore cut marks, attesting to human butchery. This is in no way especially unusual, as it is documented that dogs have periodically served as a food source among different peoples, both past and present (e.g., Snyder, 1991; Morey, 2010: 86–91).

More recently, Boudadi-Maligne et al. (2012) have reported dog remains from Le Morin rock-shelter in Southwest France. Excavated in the mid-1950s, two Late Paleolithic Magdalenian complexes were recognized, yielding 32 canid bones. Reassessment of these bones revealed that nineteen were wolf, seven were dog, and six were undetermined. These authors too were especially careful to guard against mistaking dogs for dholes. Direct dates on two teeth were 12,450 ± 55 BP and 12,540 ± 55 BP respectively, for calibrated dates falling over 14,500 years ago. The authors were struck that considerable size reduction relative to wolves was already in place, and there seems little reason to question that dog is represented.

5.2. Kesslerloch Cave, Switzerland

In the same year, Napierala and Uerpmann (2012) reported on canid remains that apparently slightly predate the

Table 5
Metric data (mm.) on several individual canid specimens under consideration, preceded by corresponding means (range immediately below mean) from certain series, for reference. See Figs. 1 and 2.

Series or specimen	Measurement[a]			Reference
	CL	GPB	LC	
Wolves				
1) *Canis lycaon* ($n = 57$)	229.7	76.2	23.91[b]	Morey 2010: 252–253
	(204–255)	(68–91)	(20.9–26.8)	
2) *C. lupus baileyi* ($n = 43$)	217.5	142.2	23.44	Morey 2010: 253–254
	(202–235)	(67–78)	(21.2–24.8)	
3) *C. lupus lupus* ($n = 10$, Denmark)	230.4	77.8	25.87	Aaris-Sørensen 1977
	(220–257)	(72–86)	(24.3–27.3)	
Dogs (*C. l. familiaris*)				Morey 2010: 259–261
European/American ($n = 65$)	150.9	54.8	16.69	
	(125–178)	(48–63)	(14.1–19.0)	
Individual Canids				
Goyet Cave 2860, Belgium	213.0	77.26	23.86	Germonpré et al., 2009; Germonpré et al. 2012: 187[d]
Mezin 5490, Ukraine	215.5	77.2	24.5	Germonpré et al., 2009; Germonpré et al. 2012: 187[d]
Mezhirich 4493, Ukraine	212.0	77.2	24.6	Germonpré et al., 2009; Germonpré et al. 2012: 187[d]
Eliseevichi I, 447, Russia	226.0	87.5	25.0[c]	Sablin and Khlopachev 2002:797
Eliseevichi I, 23781, Russia	236.0	91.0	27.3	Sablin and Khlopachev 2002:797
Předmostí 1060, Czech Republic	225.0	82.62	26.39	Germonpré et al., 2012: 187
Předmostí 1069, Czech Republic	221.0	81.86	25.66	Germonpré et al., 2012: 187
Předmostí (–), Czech Republic	217.0	83.5	24.5	Germonpré et al., 2012: 187
Razboinichya Cave, Siberia	199.0	72.0	22.6	Ovodov et al., 2011: 4

[a] Mean values for series, all in millimeters. CL = Condylobasal Length, GPB = Greatest Palatal Breadth, LC = Length of the maxillary carnassial tooth, P4. Measurements from von den Driesch (1976: 42–45). All measurements on individuals in series of 10 or more taken by the author.
[b] For the record, LC for specimen 56 (SNM512007) in Morey's (2010: 252–253) metric data on recent *C. lycaon* specimens is reported incorrectly. The correct value (23.3) is reflected here.
[c] This dimension left blank for this specimen in Sablin and Khlopachev's (2002:797) original presentation, but is reported by Germonpré et al. (2012: 187), a study on which Sablin is a participating author. Apparently that tooth was absent, and its "crown length was estimated based on its alveolar length" (Germonpré et al., 2009: 475). Accordingly, that value is reported here.
[d] Metric data provided by Germonpré et al. (2012) for canids analyzed in their 2009 publication (Germonpré et al. (2009) are only in the 2012 study.

Bonn–Oberkassel dog, from Kesslerloch Cave in Switzerland, occupied at times by Magdalenian peoples. Excavations at Kesslerloch date back to the 1870s, and yielded the upper jaw of a canid that Swiss paleontologist Ludwig Rütimeyer described as small and dog-like (Napierala and Uerpmann, 2012: 128). That maxilla is the focus of these authors' work, and was AMS dated as being just older than 14,000 years old, specifically 12,225 ± 45 BP (Napierala and Uerpmann, 2012: 134), or 14,277 ± 239 cal BP (Online CalPal). The authors' detailed description of the specimen, including measurements to compare with other canids, supports its identification as a dog. In fact, the degree of size reduction and lack of tooth crowding led the authors to suggest that "Consequently, the process of domestication, or—in biological terms—the genetic isolation between the wild wolf and the domestic dog population must have been quite advanced" (Napierala and Uerpmann, 2012: 135). Accordingly, they feel that the process of domestication surely began an undetermined length of time earlier.

5.3. Kniegrotte Cave, Germany

Kniegrotte Cave in Germany, reported by Musil as early as the 1970s (Musil, 1974, 2000), was used by Magdalenian people and yielded canid remains. Based especially on mandible and maxilla fragments from the top and middle occupational horizons, he tentatively suggested that they represented dog at an early point in the domestication process. He enumerated traits that led to this inference, including size reduction and shortened jaws, manifested modestly. Means of seven direct dates on different non-canid bones (several humanly modified) from those horizons, cluster with one exception between about 13,100 and 13,300 BP (Hedges et al., 1998: 231–232), or about 16,050 and 16,250 cal BP. The exception is an anomalously old bear bone, the only bear bone indicated, coming in at about 30,000 cal BP. Assuming that the dates close to 16,000 BP apply, the Kniegrotte case, perhaps along with the Mezin and Mezhirich skulls considered by Germonpré et al. (2009),

Table 6
Summary assessment of cases designated as Paleolithic dogs, as discussed in the text.

Site, location (no. Cases/specimens)	Age[a]	Source	Status as dogs
Goyet Cave, Belgium (1)	ca. 36,000 BP	Germonpré et al., 2009	Questionable
Razboinichya Cave, Siberia. (1)	ca. 33,000 BP	Ovodov et al., 2011	Questionable
Předmostí, Czech Republic (3)	26–27,000 BP	Germonpré et al., 2012	Questionable
Eliseevichi I, Russia (2)	ca. 17,000 BP	Sablin and Khlopachev, 2002; Germonpré et al., 2009	Questionable
Kniegrotte, Germany (4 specimens)	16,000 + BP	Musil, 1974, 2000	Transitional?
Mezin, Mezhirich, Ukraine (2)	ca. 15,000 BP	Germonpré et al., 2009	Transitional?
3 sites, France (49 specimens)	11–15,000 BP	Pioneer-Capitan et al., 2011	Credible
Le Morin, France (7 specimens)	ca. 14,600 BP	Boudadi-Maligne et al., 2012	credible
Kesslerloch Cave, Switzerland (1)	ca. 14,300 BP	Napierala and Uerpmann, 2012	Credible
Bonn-Oberkassel, Germany (1)	ca. 14,000 BP	Benecke, 1987; Nobis, 1979; Street, 2002	Credible

[a] Most age estimates based on carbon dates, in calibrated (calendar) years.

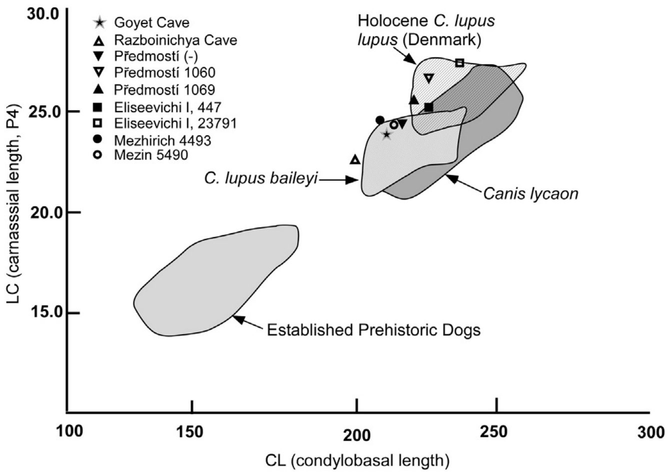

Fig. 2. Bivariate plot of LC (Length of the Carnassial, upper fourth premolar) by CL (Condylobasal Length) for three groups of modern or Holocene wolves, and a series of established prehistoric dogs, post-dating 10,000 BP, from North America and Europe (measurements defined by von den Driesch, 1976). The contours indicate the range of plotted scores for each group. Superimposed on this plot are the corresponding values for several putative Paleolithic dogs. One can see that the putative Paleolithic dogs fall within the established ranges of wolves, with two apparent exceptions (Mezhirich 4493 and the Razboinichya Cave canid. Both cases are considered in the text.

conceivably signify canids in transition, with domestication characters discernable, but not fully developed. Moreover, this possibility gains further credence from the work of Benecke (1987). As part of his DFA studies, Benecke measured and analyzed Kniegrotte specimens alongside the Bonn–Oberkassel jaw and others. While his results cast doubt on Kniegrotte and Mezin specimens as representing genuine dogs, he did note that their proximity to zoo wolves in multivariate space suggested they could represent an initial step in the domestication of the wolf.

6. Evaluation

6.1. Revised domestication timing

When writing about canid domestication timing earlier, and based on an understanding of the Bonn–Oberkassel dog as being the earliest securely identified dog at about 14,000 years ago, I suggested 15,000 BP as a reasonable estimate (Morey, 2010: 55). Adding cases covered here to the mix, an adjustment of that estimate is in order, though not a major one. The initial breeding age of a new wolf/dog may have been almost two years old, as is the case with most wild wolves (Kreeger, 2003: 193). Significantly, though, in captivity wolves may breed much sooner (Kreeger, 2003: 193). But even if first breeding age was almost two years old, that length of time would translate into dozens of generations over a mere few hundred years. And with directional selection operating, substantial changes would be in place relatively rapidly. Moreover, since lowered age at first reproduction, by many months, is characteristic of dogs versus wild wolves, generation intervals were further shortened as that change took place, apparently quickly. Thus, considerable size reduction and morphological change could take place over a relatively brief span. Initially, wild wolf genetic input into the domestic stock was likely significant, due to male wolves seeking alternative reproductive targets among free-ranging domestic females. So genetic separation was likely not in place at first, resulting in some delay in the recognizable appearance of certain domestication traits. Moreover, genetic separation was never complete, due to occasional hybridization under idiosyncratic circumstances. Therefore, allowing for modest delay in the appearance of domestication changes, 16–17,000 years ago is a reasonable estimate for the beginnings of sustained canid domestication.

Remarkably, based purely on a genetic assessment of different canids, and conditional on mutation rates, Freedman et al. (2014) have recently offered a date range of 11,000–16,000 BP for the origin of sustained canid domestication. This inference is remarkable due to the simple fact that archaeology established that time framework long ago, based only on observations of skeletal morphology and associated contextual considerations. It is unclear what purpose is served by specifying the lower number in the date range (11,000), given that, as pointed out here, several dogs have been credibly identified archaeologically that approach the upper end of the date range. Moreover, certain of the architects of the original genetics-based scenario for canid domestication occurring 100,000 or more years ago (Vilà et al., 1997), including Vilà himself, are participating authors on the most recent revised estimate that corroborates the longstanding archaeological understanding (Freedman et al., 2014).

As Larson and Bradley (2014) have recently noted, the genetics-based estimates are plagued by major inconsistencies in estimated mutation rates. For example, the year before Freedman et al.'s (2014) study, Wang et al. (2013) presented a similar study, suggesting that dogs and wolves diverged some 32,000 years ago. But as covered here, putative dogs from that time frame are not convincing, and archaeology basically confirms the upper end of the Freedman et al. (2014) time frame.

6.2. Paleolithic dogs? Some question marks resolved

There are convincing cases of Paleolithic dogs, but in keeping with the longstanding model of domestication timing, they crop up in the latter part of the Upper Paleolithic. Superficially at least, it is more exciting to envision dogs at 30,000 or more years ago than to have them only later. But later does seem to be the case. For convenience, Table 6 assembles the cases discussed here, summarizing the overall evaluation that emerges from the combined considerations. Marked uncertainty about the dating of a case possibly somewhat earlier than the credible ones indicated (ca. 19,000 cal BP?), Erralla in Spain (Vigne, 2005), precludes its consideration here (see Pionnier-Capitan et al., 2011: 2138; Boudadi-Maligne et al., 2012: 13). As Larson et al. (2012: 8878) suggested about certain of the questionable cases, they could represent "a morphologically distinct local, now-extinct population of wolves."

7. Conclusion

The longstanding archaeological understanding of sustained canid domestication timing is still largely intact, adjusted only slightly. Genetics-based estimates once ranging as old as 100,000–130,000 years ago have now been superceded by similarly derived estimates within the basic time range that archaeological work maintained many years ago. While molecular genetic work is exciting and opens many new avenues of investigation, archaeologists need not be immediately swayed by the latest developments to emanate from that direction. Archaeology, it turns out, was basically on target for a long time about a fundamental issue, and understandable eagerness to incorporate new findings from molecular genetics has led some archaeologists in an unproductive direction. On certain issues, sustained canid domestication timing being a key one, archaeology should have stuck to its guns.

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